

# Cave millipedes of the United States. XV. **Coloradesmus gen. nov. (Diplopoda, Polydesmida, Macrosternodesmidae), and four new species from caves in Colorado, USA**

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## Abstract

*Coloradesmus*, gen. nov., is established in the family Macrosternodesmidae based on *Speodesmus aquiliensis* Shear, 1984, **comb. nov.** and includes four new species: *Coloradesmus hopkinsae* sp. nov., *C. manitou* sp. nov., *C. beckleyi* sp. nov., and *C. warneri* sp. nov. All are from high altitude limestone caves in Colorado, USA, and are likely troglobionts.

## Keywords

Troglobionts, new genus, new species, new records, sphaerotrichomes

## Introduction

The generic name *Speodesmus* Loomis, 1939 has long been used for a number of small to tiny, troglobiotic polydesmidan millipedes from Texas (Elliott 2004, Elliott and Reddell 2009), New Mexico, and Colorado (Shear 1984). However, more careful

study has shown that these widely scattered species are not all components of the same genus. Shear and Reddell (2017) revived the genus name *Speorthus* Chamberlin, 1952, for two species from southeastern New Mexico and the west Texas panhandle. They also reassigned all the central Texas species nominally belonging to *Speodesmus* and the two *Speorthus* species to the family Macrosternodesmidae and discussed at length the distinctions between that family and Polydesmidae.

*Speodesmus aquiliensis* Shear, 1984, from Fulford Cave in Eagle Co., Colorado, was briefly mentioned by Shear and Reddell (2017), but no new information was provided. However, for at least ten years, prompted by extensive new collections by DBS, WAS suspected that *S. aquiliensis* and some undescribed species from Colorado caves were not congeneric with *Speodesmus echinourus* Loomis, 1943, the type species of *Speodesmus*. Here *aquiliensis* and four new species are grouped in the new genus *Coloradesmus* Shear & Steinmann.

The central Texas species remaining in *Speodesmus* need restudy and revision. Based on the study of specimens and illustrations of gonopods, there appear to be two quite distinct groups of species, and those around *Speodesmus bicornourus* Causey, 1959 may require a new generic name.

## Methods

Specimens were collected at sites around moist organic material inside the caves and field-preserved in 70–85% ethanol. Morphological studies were done using an Olympus SZH stereomicroscope and an Olympus BX50 compound microscope equipped with Nomarski optics. Gonopods were temporarily mounted on microscope slides in glycerine for detailed study up to 400X magnification. Measurements were taken using an ocular micrometer on the SZH (lengths of millipedes are highly variable because the body rings can be extended and telescoped to a considerable degree; for polydesmids, breadth of a midbody metazonite is a much better indicator of size) or relying on scale lines accompanying scanning electron micrographs. Drawings were made using an Olympus U-DA drawing tube fitted to the BX-50. Specimens were air-dried and mounted on 12.7 mm diameter aluminum scanning electron microscopy (SEM) stubs affixed with double-sided carbon conductive tape. These were sputter-coated with a 10 nm thickness layer of platinum and palladium metals using a Leica EM ACE600 high vacuum sputter coater. Scanning electron micrographs were taken with a FEI Quanta 600 FEG environmental SEM. Photographs and drawings were edited and refined using GIMP and plates were composed in InkScape.

Due to the ecological and archeological sensitivity of the caves visited for this study, coordinates for their locations are given only in general terms (minutes and seconds).

Aside from the holotype specimen of *C. aquiliensis*, all material referred to in this study has been deposited in the Denver Museum of Nature & Science, Denver, Colorado, USA.

## Taxonomy

### Family Macrosternodesmidae Brölemann, 1916

Macrosternodesmini Brölemann, 1916, p. 585.

Macrosternodesmidae Hoffman, 1980, p. 177.

The tribe was proposed by Brölemann (1916) under his “Strongylosomides” for the species *Macrosternodesmus palicolis* Brölemann, 1908, a minute, widespread synanthrope from western Europe. Hoffman (1980) raised the name to family status and listed the included genera. We think it very likely that *Chaetaspis* Bollman, 1887 (see Lewis 2002), is a senior synonym and that North America, the home of all other known *Chaetaspis* species, is the source of the synanthrope *M. palicolis*. This will be argued in detail in a forthcoming paper. In any case, the family name will remain Macrosternodesmidae under ICZN rules. For a detailed discussion of the validity of the family and its differences from, and relationship to, Polydesmidae, see Shear and Reddell (2017).

We are adopting, with slight modifications, the gonopod terminology used in Shear and Reddell (2017). Macrosternodesmine gonopods have the *prefemorite* (**pf** in Figures) densely to sparsely setose and transversely oriented to the *coxa* (**cx** in Figures). There is a prominent, sometimes bipartite *prefemoral process* (**pfp** in Figures) arising anterolaterally from the prefemorite; this process and the *acropodite* (**a** in Figures) of the gonopod are usually (but not always) separated from the prefemorite by a distinct *stem* (**s** in Figures), oriented at right angles to the prefemorite. The *acropodite* consists of a seminiferous branch on which the pore opens, often through a short or long solenite with tiny cuticular fingers or fimbriae surrounding the pore, and an *endomerite* (*sensu* Golovatch; **e** in Figures) arising near the pore or at the base of the seminiferous branch. Any portion of the acropodite distal to the pore is called the *distal zone* (**dz** in Figures). The course of the *seminal canal* (or prostatic canal; although much of the literature refers to this structure as a “groove” SEM pictures do not show it as such. It is a closed canal internal to the gonopod best seen by transmitted light microscopy. It is not clear if this canal carries sperm or merely a “prostatic” secretion. The mechanism of sperm transfer in polydesmidan millipedes remains unknown) begins mesally in the prefemorite fossa and crosses laterally to the acropodite without any loops or vesicles.

Two subfamilies are recognized: Macrosternodesminae are small, often unpigmented animals with setose metazonites and short antennae with rather bulbous distal segments, while Nearctodesminae Chamberlin & Hoffman 1950 are larger, have smooth red, pink or brown metazonites and long antennae with cylindrical distal segments. See Shear and Reddell (2017) for lists of genera belonging to each subfamily. Recently, Shear and Shelley (2019) added a new genus *Packardesmus* (type species *Polydesmus cavicola* Packard, 1877) to the subfamily Macrosternodesminae.

Macrosternodesmine species are usually 2.5–12 mm long, unpigmented and with narrow, toothed paranota. The collum and metazonites bear three rows of setae set

on more or less distinct tubercles, or densely scattered setae not arranged in rows and not on obvious tubercles; the setae may be long and acute or short and clavate. The epiproct (telson) is short-triangular with four spinnerets in a shallow depression. The legs of males have podomeres (coxae, prefemora and femora) that are enlarged, dorsally swollen, and set with sphaerotrichomes. Antennomere six is enlarged and longer than antennomere five. The majority of North American species in this subfamily have been collected exclusively in caves, mostly west of the Mississippi Valley.

### ***Sphaerotrichomes***

Sphaerotrichomes are unusual, enigmatic structures that occur on some or all podomeres of many species of polydesmoidean and dalodesmoidean millipedes (Fig. 4). Typically sphaerotrichomes are found only on the legs of males. They consist of a spherical base set in a socket, with a pointed projection, resembling a more typical seta, extending distally (toward the tip of the leg) from a sharp demarcation with the spherical base. Mesibov (2004) has documented four distinct types of sphaerotrichome from Australian dalodesmids. The shape of the spherical base varies from a more typical and widespread rounded, slightly pyramidal form to more nearly spherical, and the surface can be either smooth or with evenly spaced, concentric ridges, or with an apical dimple. The seta-like projection may be absent, short and acute, long and slightly curved at the tip, or with an expanded tip, according to the SEMs published by Mesibov (2004, figs 1A–D). Only a few species of North American polydesmids and macrosternodesmids have been examined for these structures using SEM. In the polydesmids, the enlarged anterior legs of the males are densely setose, and what may be vestigial sphaerotrichomes are scattered amongst the setae. In the macrosternodesmids, setae of the ventral leg surfaces are suppressed and sphaerotrichomes are large and prominent. There appears to be little variation, with distinctly rimmed sockets, subpyramidal, ridged bases and relatively short, acute setal projections. Mesibov (2004) has suggested that the distribution and form of sphaerotrichomes may be of phylogenetic importance, and we agree. A survey of these structures in a wide range of taxa would be extremely useful.

There have been no ultrastructural studies of sphaerotrichomes using transmission electron microscopy, and they are not mentioned in a recent review of millipede sense organs as such (Müller and Sombke 2015). Their function remains unknown, but since they are found only in males, some connection to sexual behavior may be inferred.

### ***Coloradesmus* gen. nov.**

<http://zoobank.org/7D2A725E-B05E-4124-9744-6A2BE883EA0F>

**Type species.** *Speodesmus aquiliensis* Shear, 1984.

**Diagnosis.** Distinct from the similar *Pratherodesmus* Shear, 2009 in its much larger gonopod solenomere and endomerite, from *Tidesmus* Chamberlin, 1943, *Sequoiaedesmus* Shear & Shelley, 2008 and *Nevadesmus* Shear, 2009 in having a simple,

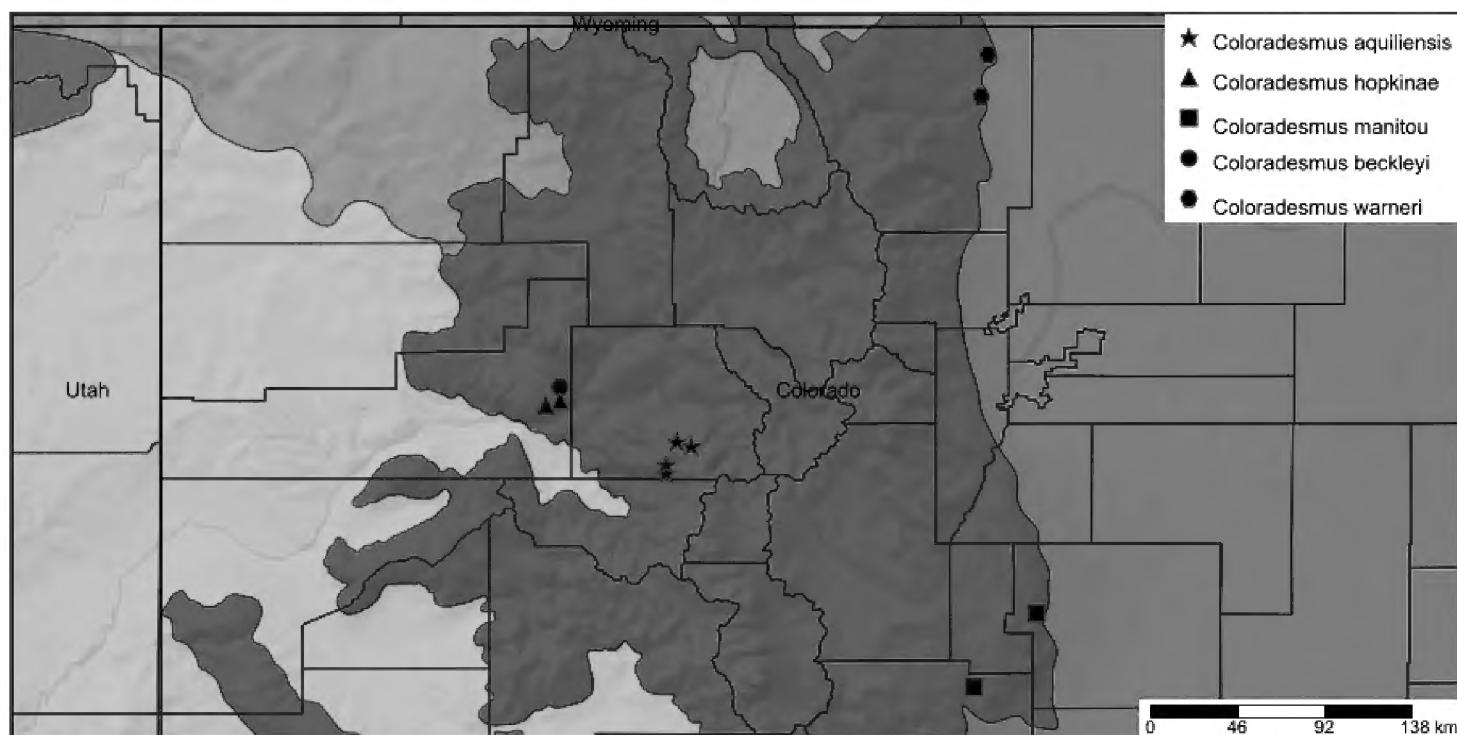
unbranched endomerite, or endomerite lacking. *Packardesmus* Shear & Shelley, 2019 has all gonopod branches clustered at the tip of an extended prefemoral stem.

**Description.** Small, probably troglobiotic macrosternodesmiles 4.0–11.0 mm long, lacking pigment. Nineteen trunk rings (collum + 17 pedigerous rings + telson). Head sparsely to densely setose. Antennae (Fig. 22) relatively short, elbowed between antennomeres three and four, antennomere six much enlarged, with subapical accessory sensory organ. Order of length of antennomeres: 6>3=4>5>2>7>1>8. Collum with three rows of eight setae (number may vary on more posterior rings); anterior row at anterior margin of collum, middle row may be dispersed, posterior row at posterior margin of collum. Collum setae on low tubercles or sockets more or less flush with surface. Subsequent rings with anterior row posterior to anterior margin of metazonite, but posterior row at posterior edge of metazonite, rows of 6–10 setae or setae becoming more scattered on more posterior rings. Metazonites with narrow paranota bearing three short, marginal teeth corresponding to setal rows, posterolateral metazonite corners acute to projecting. Limbus minutely dentate. Ozopores laterodorsal, at posterolateral corners, opening in a distinct pore callus. Pore formula 5, 7, 9, 10, 12, 13, 15–18. Penultimate ring with 10–18 scattered setae, telson with 8–10 scattered setae, epiproct process short, blunt, with four spinnerets set in shallow depression. Paraprocts and hypoproct with two setae. Dorsal setae post-collum on more prominent tubercles, setae themselves may be long, acute, or short, clavate. Males with all legs having dorsally swollen prefemora, femora also dorsally swollen, curved, both podomeres ventrally with many sphaerotrichomes; postfemora and tibiae normal, with few ventral sphaerotrichomes or sphaerotrichomes absent (Fig. 4). Gonopod socket rounded-cordate, often with anterior rim, midposterior portion extending slightly between ninth coxae. Gonopods joined by tough membrane anteriorly; small, more sclerotized strip represents sternal remnant, articulates mesally with coxae. Gonopod coxae not movable, tightly appressed in midline but not fused, anteriomesally excavate to receive telopodite. Telopodites movable only in plane parallel to body axis. Prefemorites transverse across posterior surface of coxae. Prefemoral process single, broad, prefemoral process and acropodite on short stem arising from prefemrite. Acropodite with long seminiferous branch, pore surrounded by minute cuticular extensions, these sometimes extending distad along concave mesal surface of distal zone. Distal zone long, tapering, acute, or short, blunt. Endomerite arising basally or midway on acropodite.

**Etymology.** From the state of Colorado, to which the genus appears endemic, and the common combining stem *-desmus* in the order.

**Species included.** In addition to the type species, the following new species: *beckleyi*, *warneri*, *hopkinsae* and *manitou*.

**Distribution.** See Map 1. Caves in central and northern Colorado, USA. Species distributions appear to be defined by major rivers and large canyons. Groaning Cave where *C. hopkinsae* occurs is across Deep Creek Canyon from La Sunder Cave where *C. beckleyi* occurs and this canyon is 2,000' deep. The Colorado River may define the limits of *C. aquiliensis* relative to *C. beckleyi* and *C. hopkinsae* because *C. aquiliensis* has only been collected south of the Colorado River, while the other two species were



**Map 1.** Northwestern Colorado, showing the distribution of *Coloradesmus* species. Green area indicates Colorado Rocky Mountain Forest Ecoregion. Symbols may represent more than one locality as some caves are very close to one another. Stars, *C. aquiliensis*, triangles, *C. hopkinsae*, squares, *C. manitou*, circles, *C. beckleyi*, hexagon, *C. warneri*.

collected north of the river. It is likely that *Coloradesmus* will extend into Wyoming because *C. warneri* was collected 5 miles from the state line.

**Notes.** Two species groups are recognizable in this genus, distinguished primarily by size and the presence or absence of a distinct endomerite. *Coloradesmus aquiliensis*, *C. hopkinsae* and *C. manitou* are 0.6 mm or greater in width and from 5–11 mm long, depending on the contraction or extension of the body. *Coloradesmus beckleyi* and *C. warneri* are considerably smaller, about 0.4 mm wide and 4 mm long, placing them among the smallest of all millipedes. The former three species have distinct endomerites, while endomerites seem lacking in the latter two. Division of *Coloradesmus* may prove desirable in the future but for now we prefer to group all the species in a single genus.

All specimens of *Coloradesmus* were collected in the dark zones of limestone caves. The preferred habitat for the genus appears to be caves with moist organic materials including wood, scat and guano. Millipedes representing *Coloradesmus* were found under rocks, burrowing in cave soils, and on wet cave formations. Many of the caves where *Coloradesmus* occurs are remote and at high-altitudes with temperatures of 2–4 °C.

Establishing troglobiosis is difficult in macrosternodesmines due to the small size and depigmented appearance of nearly all species except those of *Tidesmus*. Eyelessness is not a marker of troglobiotic adaptation in Polydesmida, since all known species of the order, some thousands, are eyeless. However, despite antennae and legs that seem not much elongated compared to those of litter-dwelling species of *Chaetaspis*, the species of *Coloradesmus* have a loose-jointed, elongated appearance as a whole that, along with the weak sclerotization of the rings, suggests a significant degree of adaptation.

As WAS has repeatedly emphasized in previous publications, collecting in caves has generally been more intense than surface collecting, especially in western parts of the United States. Further, suspect troglobionts tend to be very small and would only be

found outside caves by very careful sifting of forest litter at an appropriate season of the year, if they exist there. Many caves in the Rocky Mountains are at high altitudes or are situated in surroundings that would not be very conducive to the survival of small, delicate arthropods on the surface. The mesovoid space of small cavities from a few centimeters to meters underground has not been explored by collectors in western North America.

### Key to species

- 1      Width of midbody metazonites 0.6 mm or greater; metazonital setae acute **2**
- Width of midbody metazonites 0.4 mm or less; metazonital setae blunt, subclavate..... **4**
- 2      Distal zone of gonopod short, blunt; endomerite distinctly elbowed.....  
..... *C. manitou*
- Distal zone of gonopod long, tapering, acute; endomerite very short or not elbowed ..... **3**
- 3      Endomerite short, perhaps seemingly absent, but tightly appressed to prefemoral process; prefemoral process broadly spatulate, with lateral subapical tooth..... *C. hopkinsae*
- Endomerite long, obvious; prefemoral process scoop-like, without a tooth ...  
..... *C. aquiliensis* (Shear)
- 4      Prefemoral process with thin, pointed tip; distal zone bent laterally at right angle or less..... *C. beckleyi*
- Prefemoral process broad at tip; distal zone evenly continuing line of acropodite..... *C. warneri*

### *Coloradesmus aquiliensis* (Shear, 1984), comb. nov.

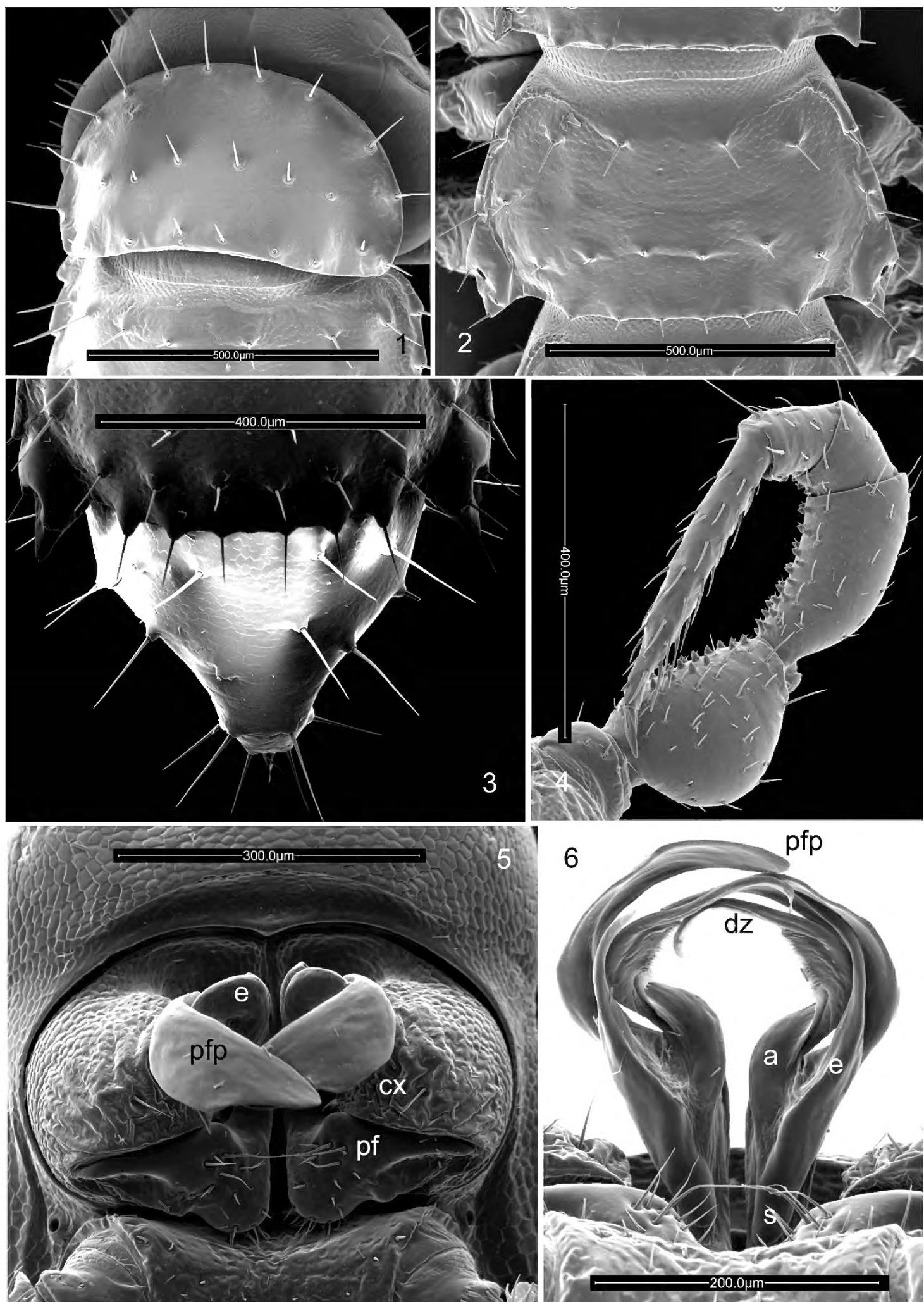
Figs 1–8

*Speodesmus aquiliensis* Shear, 1984, p. 96.

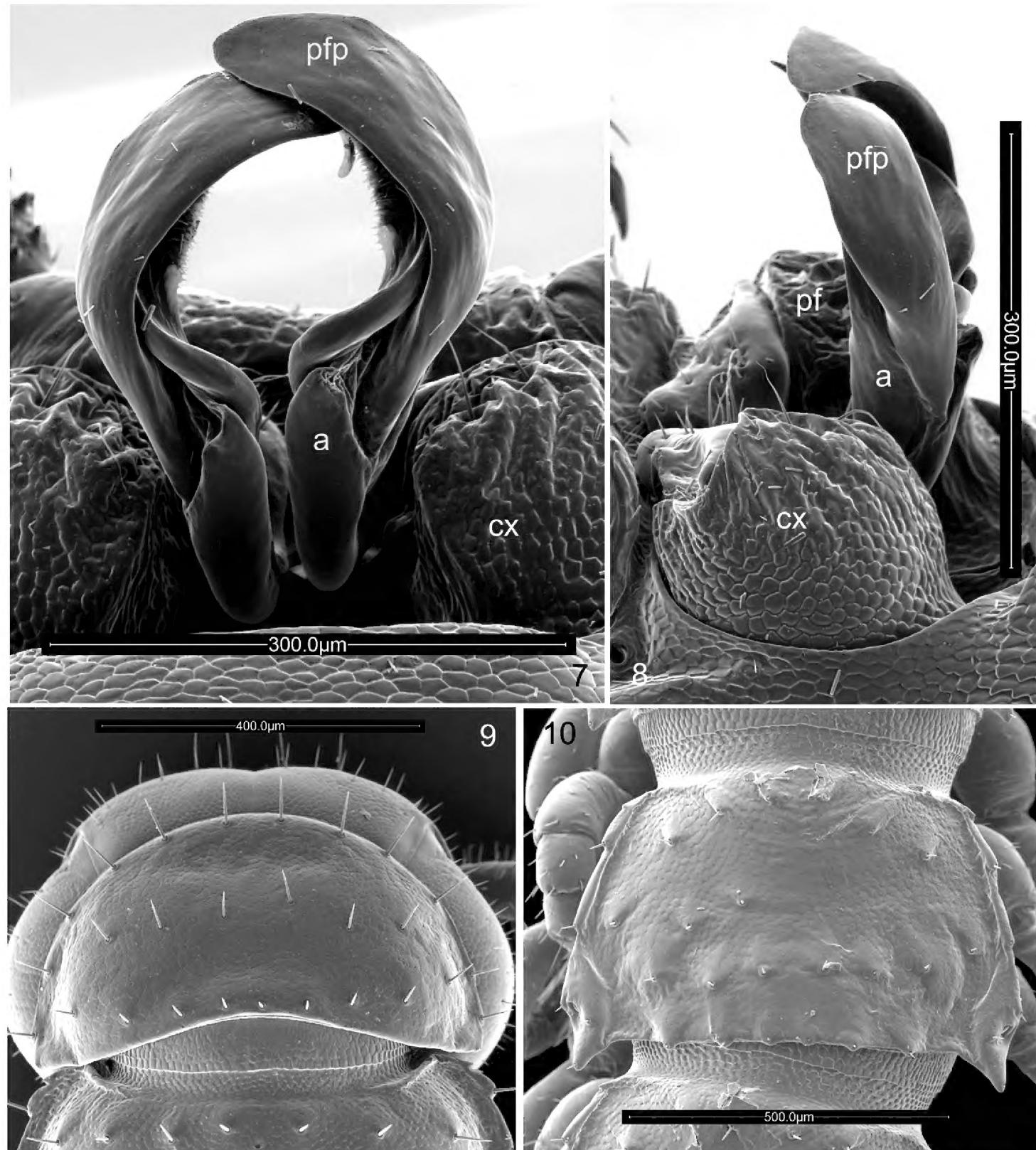
**Types.** Male holotype (American Museum of Natural History) from Fulford Cave, 21 mi SE of Eagle, Eagle Co.: Colorado, collected 6 July 1980 by J. R. Holsinger et al.

**Diagnosis.** A larger species of *Coloradesmus* distinguished by details of the gonopods; in *Coloradesmus hopkinsae* the prefemoral process is much broader and has a laterodistal tooth. *Coloradesmus manitou* differs from *C. aquiliensis* in the endomerite, which in *manitou* emerges from the acropodite at nearly a right angle, then turns sharply distad. *Coloradesmus beckleyi* and *C. warneri* are only half the length of the other three known species of the genus.

**Corrections to original description.** With the characters of the genus. Lengths of a series of specimens from Fulford Cave, the type locality, varied from 4.5–6.2 mm, the longer specimens strongly extended. Setae on collum, metazonites and telson long, acute. In the description of the gonopods, the prefemoral process is erroneously de-



**Figures 1–6.** *Coloradesmus aquiliensis* male. **1** Collum, dorsal view **2** midbody ring, dorsal view **3** telson, dorsal view **4** right leg 7, posterior view **5** gonopods, ventral view **6** gonopods, posterior view. See text for explanation of labels.



**Figures 7–10.** *Coloradesmus* species males. **7** *C. aquiliensis* gonopods, anterior view **8** *C. aquiliensis* gonopods, lateral view **9** *C. hopkinae* collum, dorsal view **10** *C. hopkinae* midbody ring, dorsal view. See text for explanation of labels.

scribed as bifid and the endomerite is shown in the drawings as attached to the prefemoral process, giving that impression.

**Records.** COLORADO: Eagle Co.: Fulford Cave, 10,000' asl, organic matter in packrat midden, 39°29'N, 106°33'W, 22 June 1999, 7 males, 13 females (topotypes); Devil's Den Cave, 11,500' (3506 m) asl, 35°F, under stones and logs in dark zone, 39°30'N, 106°37'W, 25 August 1999, 18 males, 7 females, juveniles; Herbie's Deli Cave, 9200' asl, under rocks in dark zone, 40°01'N, 105°40'W, 31 August 2003, mf; 15 August 2007, 2 males; Lime Creek Cave, 9200' (2804 m) asl, 40°00'N, 105°40'W, 5 September 2001, 2 males.

***Coloradesmus hopkinsae* Shear & Steinmann, sp. nov.**

<http://zoobank.org/12C578A0-7C71-4D06-8462-C558394F3046>

Figs 9–15

**Types.** Male holotype and male paratypes from Colorado, Garfield Co.: Bair Cave, 9800' asl, 39°38'N, 107°14'W, 200 ft from entrance, collected September 1998 and 19 June 1999 by D. Steinmann.

**Diagnosis.** Similar in somatic characters to both *C. aquiliensis* and *C. manitou*, but differing from both in the broader, more irregularly shaped prefemoral process of the gonopods, and in having a short endomerite tightly appressed to the prefemoral process.

**Etymology.** The species is named in honor of Kay Hopkins of the United States Forest Service for her contributions to cave conservation, cave research and cave preservation.

**Description. Male holotype.** Length about 7.0 mm, greatest width 0.66 mm. With the characters of the genus. Head sparsely setose. Basal joint of mandibles not greatly exceeding width of collum; front margin of collum evenly arcuate, posterior margin shallowly embayed (Fig. 9). Setae of collum and metazonites acute throughout (Figs 9–11), setal rows of metazonites sometimes interrupted, supplemental setae sometimes present (Fig. 10). Setal tubercles become more prominent posteriorly (*cf.* Figs 10, 11). Telson rounded, with two distinct rows of setae; epiproct blunt (Fig. 11). Gonopod socket occupies entire width of prozonite, subcordate, indenting ninth sternite (Fig. 12). Gonopods with robust acropodite (a, Fig. 13), ending in long, acute distal zone (dz, Figs 13, 14); seminal pore long, with many tiny finger-like cuticular projections (Fig. 15); endomerite (e, Fig. 13) short, tightly appressed to prefemoral process. Prefemoral process (pfp, Figs 13, 14), large, broad, scoop-shaped, with subapical lateral tooth, tip acute, slightly lobed.

**Distribution.** COLORADO: Garfield Co.: Groaning Cave, 39°42'N, 107°10'W, 9800' (2804 m) asl, 9 October 2008, D. Steinmann, male, females, juveniles.

***Coloradesmus manitou* Shear & Steinmann, sp. nov.**

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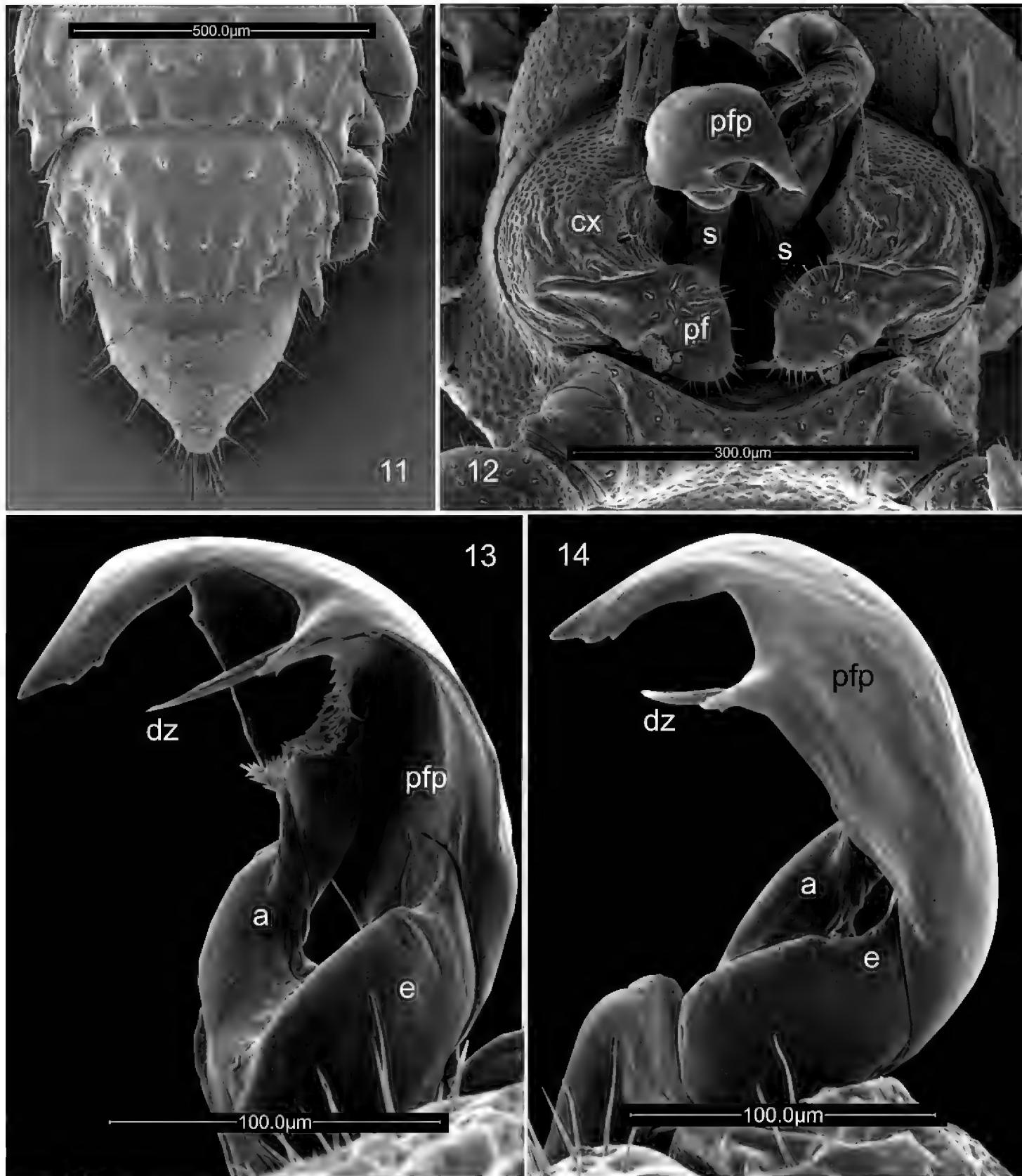
Figs 16–21

**Types.** Male holotype and many male and female paratypes from Manitou Cave, El Paso Co.: Colorado, 7000' asl, collected 3 August 1996, by D. Hubbard.

**Diagnosis.** A larger species, like *C. aquiliensis* and *C. hopkinsae*, but differing in that the metazonital setal tubercles are very low and often scattered across the metazonite, not in rows. The gonopod endomerite is stouter than in *C. aquiliensis* and emerges from the acropodite at almost a right angle, then turning distad; the distal zone is shorter and often curved. Unlike *C. hopkinsae*, the gonopod pore is compact with few cuticular projections.

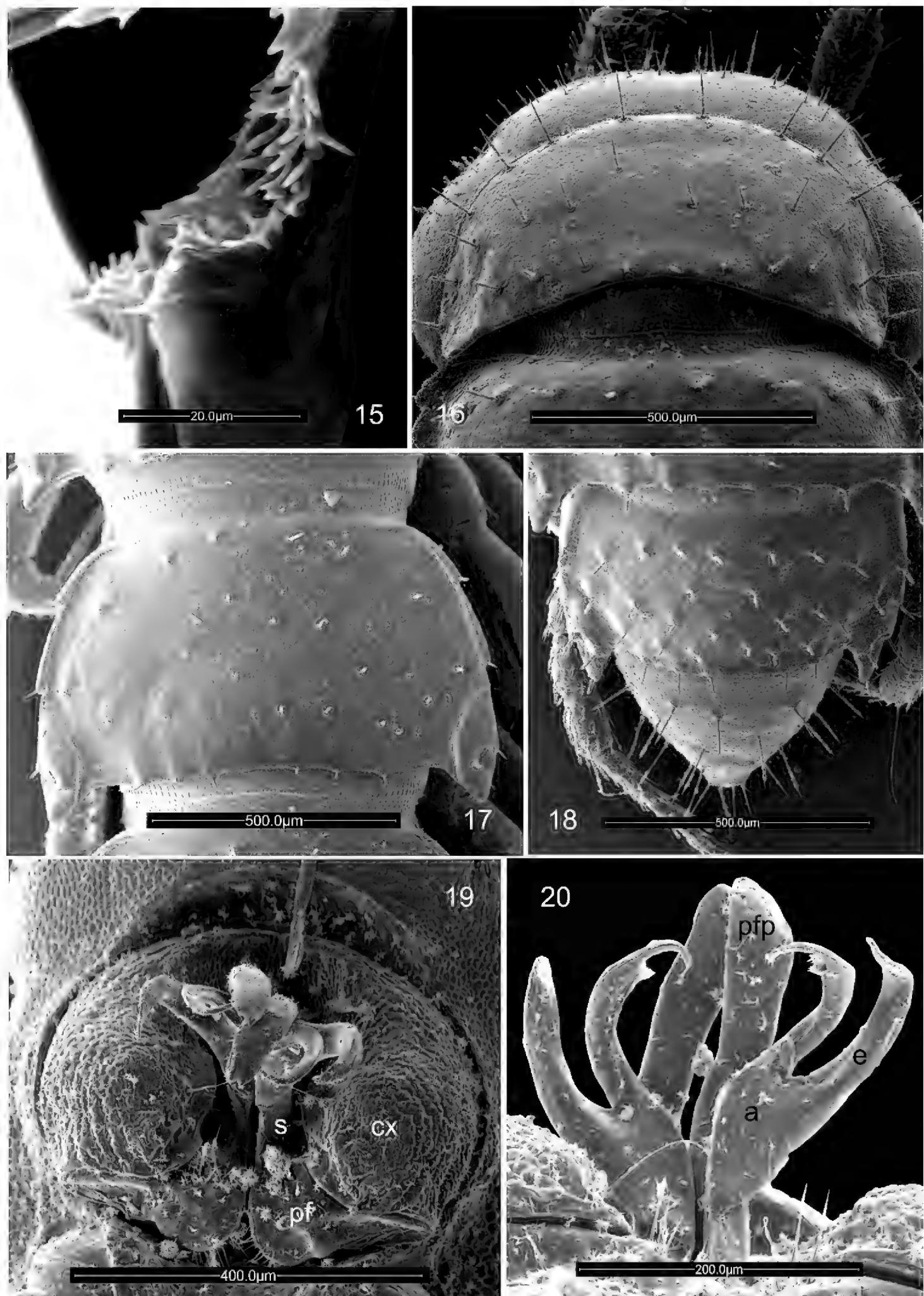
**Etymology.** The species epithet is a noun in apposition, after the type locality.

**Description. Male paratype.** Length 8.0–10.5 mm, depending on degree of extension, greatest width 0.9 mm. With the characters of the genus. Head densely se-



**Figures 11–14.** *Coloradesmus hopkinae* male. **11** Telson, dorsal view **12** gonopods, ventral view **13** right gonopod, mesal view **14** right gonopod, medioposterior view. See text for explanation of labels.

tose, basal joint of mandibles slightly exceeding width of collum (Fig. 16). Collum with three rows of long, acute setae (Fig. 16). Midbody metazonites nearly smooth, setal tubercles low to absent; setae becoming shorter posteriorly (Fig. 17), rows disrupted so that setae may appear scattered. Telson with 12–15 long, acute, scattered setae, rounded, epiproct hardly distinct. Gonopod socket occupying entire width of prozonite, nearly circular with strong projecting anterior margin, not indenting sternite nine (Fig. 19). Gonopods with subhemispherical coxae (cx, Fig. 19) immovable, completely filling socket; acropodite arises on distinct stem (s, Fig. 19); prefemoral process relatively narrow, margins even, not scoop-like (pfp, Figs 20, 21); acropodite



**Figures 15–20.** *Coloradesmus* species males. **15** *C. hopkinae*, gonopod seminal pore **16–20** *C. manitou* **16** collum, dorsal view **17** midbody ring, dorsal view **18** telson, dorsal view **19** gonopods, ventral view **20** Gonopods, posterior view. See text for explanation of labels.

(a, Figs 20, 21) robust, distal zone (dz, Fig. 21) short, strongly curved; endomerite (e, Figs 20, 21) nearly as large, robust as acropodite, at wide angle to acropodite.

**Female paratype.** Closely similar to male in all nonsexual characters.

**Distribution.** COLORADO: Fremont Co.: Fly Cave, 7 August 1996, D. Hubbard, 2 males; Marble Cave, 7 August 1996, D. Hubbard, 7 males and 8 females (these two caves are nearly adjacent at  $38^{\circ}36'N$ ,  $105^{\circ}13'W$  (1982 m) asl; El Paso Co.: Cave of the Winds, 7000' (2134 m) asl,  $38^{\circ}55'N$ ,  $104^{\circ}55'W$ , 2 August 1996, D. Hubbard, 10 males, 6 females and 20 February 2007, David Steinmann, 6 males, 6 females; Dilatation Cave, 7400' (2256 m) asl,  $38^{\circ}48'N$ ,  $104^{\circ}52'W$ , 19 June 2009, D. Steinmann, male; Pedro's Cave, 6800' (2073 m) asl,  $38^{\circ}55'N$ ,  $104^{\circ}55'W$ , 5 January 2008, D. Steinmann, male, females, juveniles.

### *Coloradesmus beckleyi* Shear & Steinmann, sp. nov.

<http://zoobank.org/9737DDFE-2F14-4F5A-96FF-8E47BB053387>

Figs 22–28

**Types.** Male holotype and male and female paratypes from La Sunder Cave, Garfield Co.: Colorado, 7500' (2287 m) asl,  $39^{\circ}42'N$ ,  $107^{\circ}10'W$ , in organic matter and under cardboard along the first 1000' of passage, collected 31 July 1999 by D. Steinmann.

**Diagnosis.** A small species of *Coloradesmus*, as is the following species, but differing from *C. warneri* in details of the gonopods, as shown in Figs 28–29.

**Etymology.** The species epithet honors Steve Beckley, for his dedication to cave conservation and education as the owner of Glenwood Caverns in nearby Glenwood Springs.

**Description. Male holotype.** Length, about 4 mm, greatest width 0.4 mm. Head with short, sparse setae; basal joint of mandible exceeding width of collum (Fig. 22). Collum relatively short, posterior margin evenly, concavely curved (Fig. 23); collum setae short, clavate. Metazonites with somewhat suppressed but distinct paranota bearing obsolete teeth (Figs 22–25); setae distinctly clavate, short, set on prominent tubercles, rows even, uninterrupted. Telson (Fig. 25) with few setae, epiproct indistinct. Gonopods (Figs 26–28) with coxae rather oval, immovable; acropodite (a, Figs 26–28) robust, blocky, pore without cuticular fimbriae, endomerite evidently absent. Prefemoral process (pfp, Figs 26–28) exceeding acropodite, narrow, with distinct acute hook at tip.

**Female paratype.** Similar in all nonsexual characters to male.

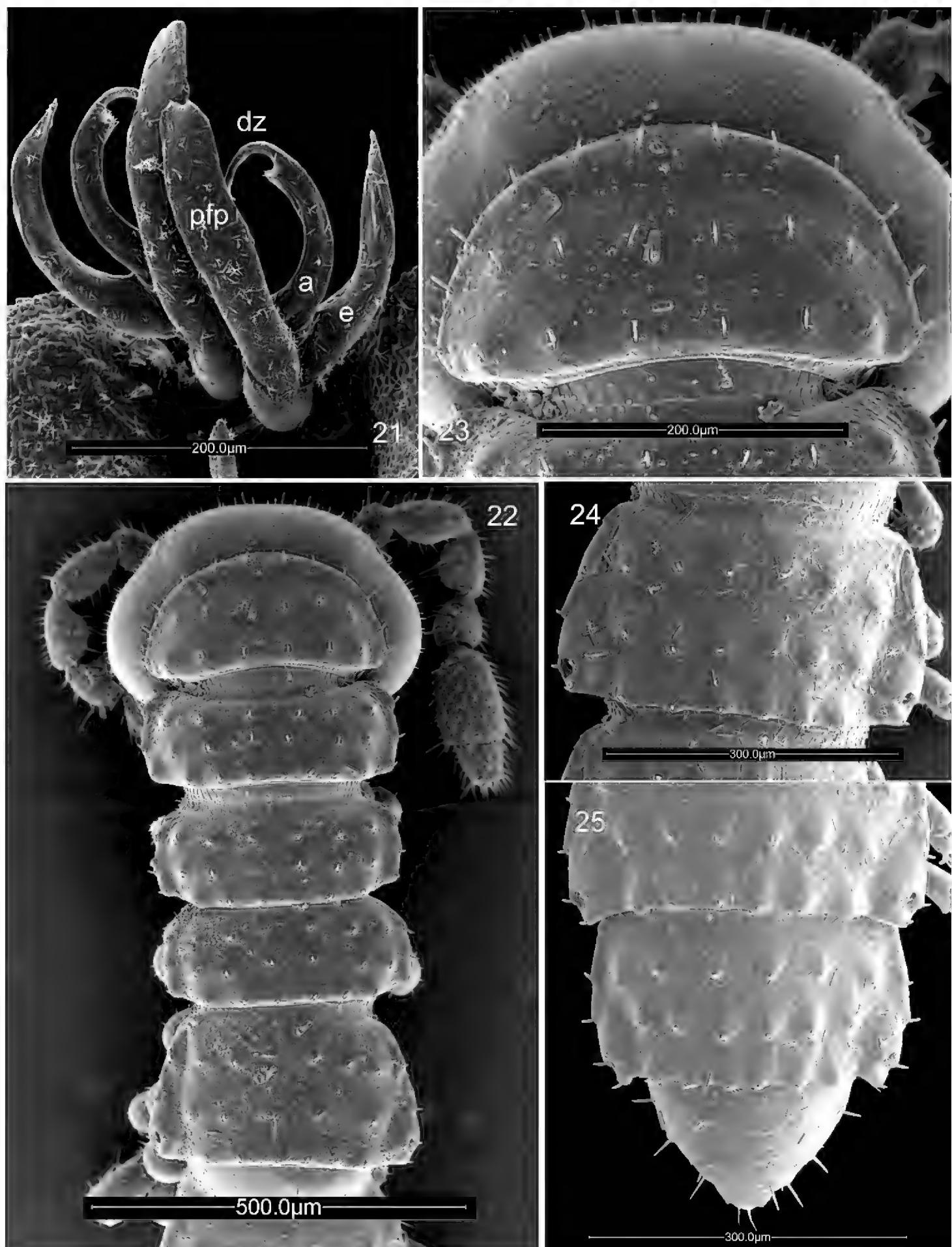
**Distribution.** Known only from the type locality.

### *Coloradesmus warneri* Shear & Steinmann, sp. nov.

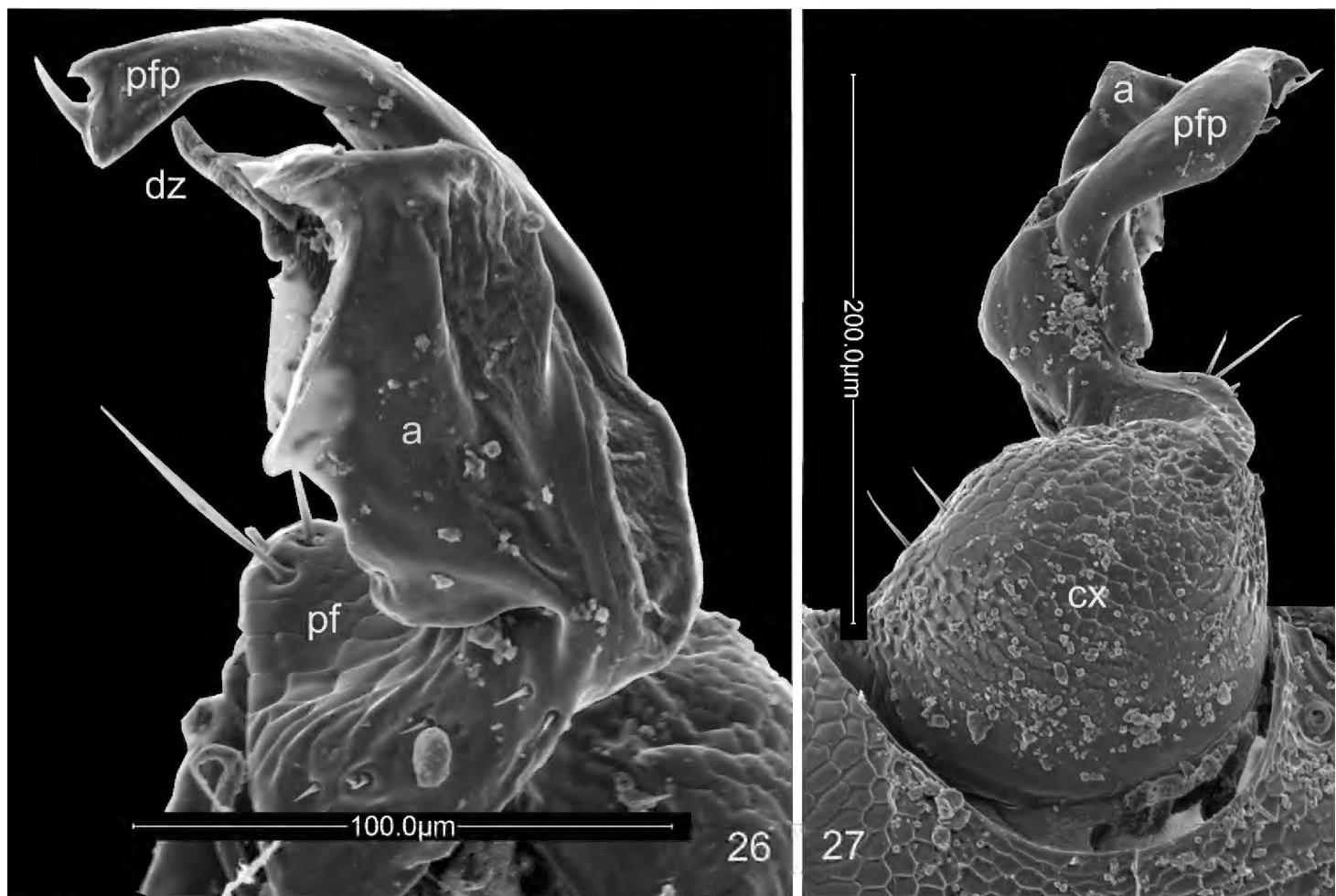
<http://zoobank.org/6D68C4EF-3755-4347-8D5E-F26CE56CE7EF>

Fig. 29

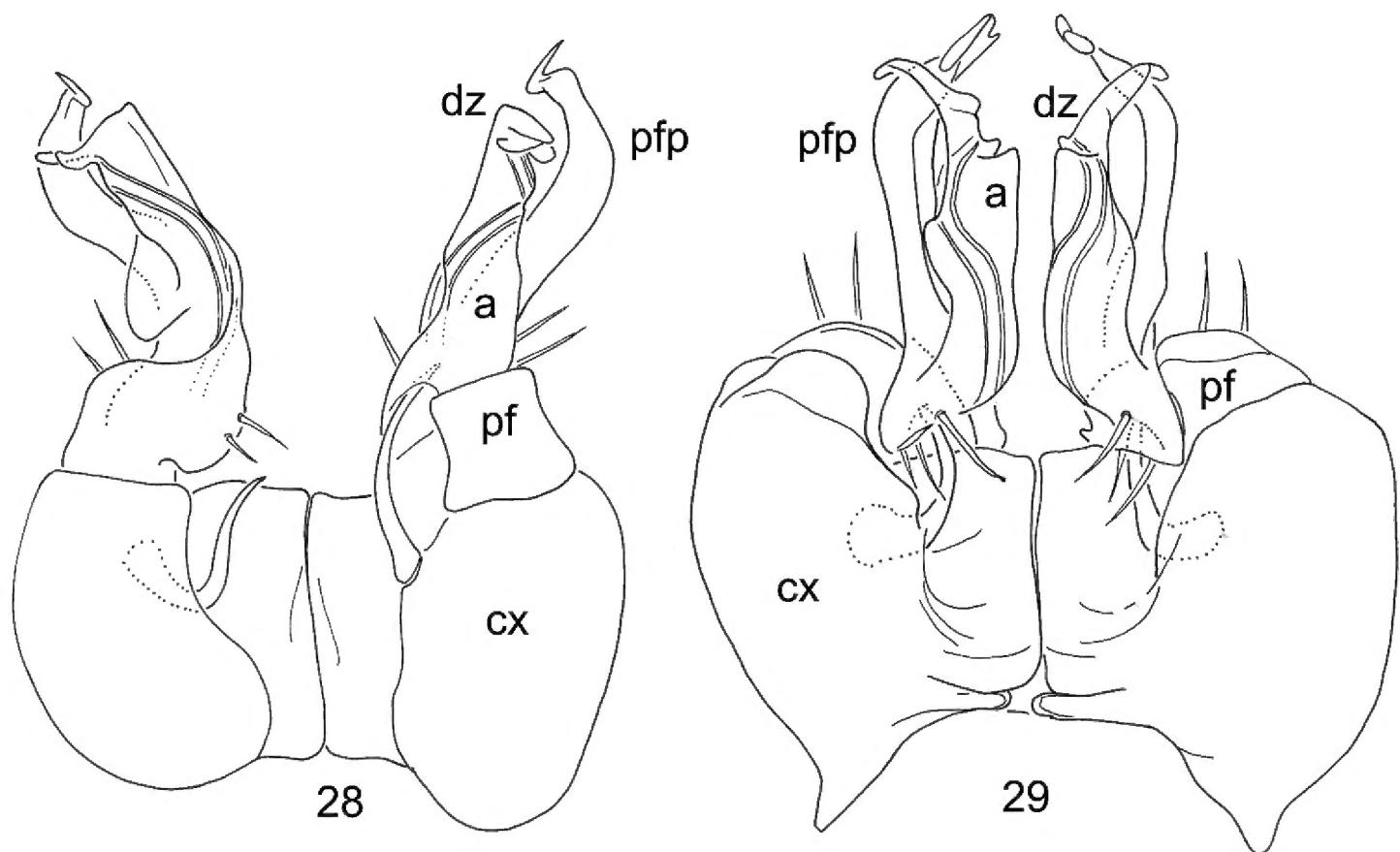
**Types.** Male holotype and female paratype from White Water Cave, 6100' (1860 m) asl,  $40^{\circ}54'N$ ,  $105^{\circ}09'W$ , Larimer Co.: Colorado, collected 1 June 2007 by D. Steinmann.



**Figures 21–25.** *Coloradesmus* species males. **21** *C. manitou* gonopods, posterior view **22–24** *C. lasunda* male **22** head, collum and anterior four rings, dorsal view **23** collum, dorsal view **24** midbody ring, dorsal view **25** telson, dorsal view. See text for explanation of labels.



**Figures 26, 27.** *Coloradesmus lasunda* male. **26** Right gonopod, mesal view **27** right gonopod, lateral view. See text for explanation of labels.



**Figures 28, 29.** *Coloradesmus* species gonopods, posterior views. **28** *C. lasunda* **29** *C. warneri*. See text for explanation of labels.

**Diagnosis.** Very similar in nonsexual characters to the foregoing species, but differing in details of the gonopods. Compare Figs 28, 29.

**Etymology.** The species epithet honors Ed Warner, an active conservationist and donor to the Denver Museum of Nature & Science, for his dedication to nature and the environment.

**Description.** In size and in nonsexual characters, this species is nearly identical to *Coloradesmus beckleyi*. Gonopods (Fig. 29) with large subhemispherical coxae immovable in gonopod socket. Acropodite (a, Fig. 29) long, relatively slender, not blocky, slightly curved. Pore lacking cuticular filaments. Distal zone (dz, Fig. 29) curved laterad, tapering, not bent at an angle; prefemora process (pfp, Fig. 29) slender, tapering, gradually curved.

**Female paratype:** Similar in all nonsexual characters to male.

**Distribution.** COLORADO: Larimer Co.: White Water Cave, 3 November 2006, D. Steinmann, juveniles; Kremer's Cave, 40°45'N, 105°10'W, 5600' (1707 m) asl, dark zone, 12 August 2006, D. Steinmann, male; 29 March 2008, D. Steinmann, juveniles; Signature Cave, 40°75'N, 105°11'W, 6100' (1860 m) asl, 22 February 2011, D. Steinmann, male, juveniles; 22 October 2011, D. Steinmann, male, female, juveniles.

**Notes.** Females of a species of the European genus *Polydesmus* were collected along with the types in Whitewater Cave. All species of *Polydesmus* recorded from North America are anthropochoric.

## Unassigned specimens

The following specimens appear to belong to *Coloradesmus* but could not be identified to species because of the absence of males. Future collecting in these caves should focus on obtaining male specimens. COLORADO: Eagle Co.: Hourglass Cave, 10000' (3050 m) asl, station 41/45, 1999, C. Mosch, female; Cattleguard Cave, 8000' (2439 m) asl, 4 September 2006, juveniles (2 vials). El Paso Co.: Swirling Mists Cave, 7000' (2134m) asl, , 5 January 2008, D. Steinmann, female.

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## References

- Brölemann HW (1908) Description d'un genre nouveau et d'une espèce nouvelle de myriapodes de France. Bulletin de la Société Entomologique de France 1908(7): 94–96. <https://doi.org/10.5962/bhl.part.5606>
- Brölemann HW (1916) Essai de classification des polydesmides (Myriapodes). Annales de la Société Entomologique de France 84: 523–608. <https://doi.org/10.5962/bhl.part.24168>
- Causey NB (1959) Two new troglodytic millipedes from Texas. Proceedings of the Biological Society of Washington 72: 69–74.
- Chamberlin RV (1952) Three cave-dwelling millipedes. Entomological News 63: 10–12.
- Elliott WR (2004) *Speodesmus* cave millipedes. Four new species from central Texas (Diplopoda: Polydesmida: Polydesmidae). Texas Memorial Museum Speleological Monographs 6: 163–174.
- Elliott WR, Reddell JR (2009) New records of *Speodesmus* (Diplopoda: Polydesmida: Polydesmidae) from Fort Hood, Bell and Coryell Counties, Texas. Texas Memorial Museum Speleological Monographs 7: 147–150.
- Lewis JJ (2002) *Chaetaspis aleyorum*, a new species of millipede from Tumbling Creek Cave, Missouri, with a synopsis of the cavernicolous species of *Chaetaspis* (Diplopoda: Polydesmida). Myriopodologica 7: 101–111.
- Loomis HF (1939) The millipedes collected in Appalachian caves by Mr. Kenneth Dearolf. Bulletin of the Museum of Comparative Zoology 86: 165–193.
- Müller CHG, Sombke A (2015) 9 Diplopoda-sense organs. In: Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda, vol 2, Minelli A, Ed., Brill, Leiden, 181–236. [https://doi.org/10.1163/9789004188273\\_010](https://doi.org/10.1163/9789004188273_010)
- Shear WA (1984) Cave millipedes of the United States. III. Two new species from the western states (Diplopoda: Polydesmida, Chordeumatida). Myriopodologica 1: 95–97.
- Shear WA, Reddell JR (2017) Cave millipedes of the United States. XIV. Revalidation of the genus *Speorthus* Chamberlin, 1952 (Diplopoda, Polydesmida, Macrosternodesmidae), with a description of a new species from Texas and remarks on the families Polydesmidae and Macrosternodesmidae in North America. Insecta Mundi, 0529, 1–13.
- Shear WA, Shelley RM (2007) The millipede genus *Tidesmus* Chamberlin, 1943 (Polydesmida, Macrosternodesmidae). Zootaxa 1656, 51–68. <https://doi.org/10.11646/zootaxa.1656.1.2>
- Shear WA, Shelley RM (2008) Cave millipedes of the United States. VI. *Sequoiadesmus krenae*, n. sp., from Sequoia and Kings Canyon National Parks, California, USA (Diplopoda, Polydesmida, Polydesmidae, Macrosternodesmidae). Zootaxa 1693: 41–48. <https://doi.org/10.11646/zootaxa.1693.1.3>

Shear WA, Shelley RM (2019) Solved after 140 years: the identity of the millipede *Polydesmus cavicola* Packard, 1877, and proposal of *Packardesmus* n. gen. (Diplopoda: Polydesmida: Macrosternodesmidae). Zootaxa 4559: 184–190. <https://doi.org/10.11646/zootaxa.4559.2.11>

Shear WA, Taylor SJ, Wynne JJ, Krejca JK (2009) Cave millipedes of the United States. VIII. New genera and species of polydesmidan millipedes from caves in the southwestern states (Diplopoda, Polydesmida, Macrosternodesmidae). Zootaxa 2151: 47–65.